3

Head Muscles of *Boa constrictor*

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(Text-figures 1 & 2)

Introduction

THIS paper presents a complete description of the head muscles of *Boa constrictor,* including muscle form, origin, insertion, location, variations and to a lesser extent function and innervation. This will serve as a basis for comparison of the head muscles of the other American boids and, eventually, all Boidae. *Boa constrictor* was chosen for basic description because of its generalized form, large size and availability.

Morphological studies on snakes have usually taken one of two approaches; either (1) an organ has been described in a number of different, and often unrelated, species (*i.e.,* lungs, Brongersma, 1951; hemipenes, Dowling & Savage, 1960; trigeminal musculature, Lakjer, 1926) or (2) some aspect of the anatomy has been described thoroughly in a single species (*i.e.,* jaw muscles, Cowan & Hick, 1951; Albright & Nelson, 1959; circulation, Jacquart, 1855; Ray, 1934). These and many similar, essential works, do not complete our understanding of snake morphology. No particular internal structure has been studied throughout a taxonomic group, so it is not known what amount of variation is normal and what is of specific, generic or familial importance. Often it is not known that a structure on which a taxonomic group is partially based actually exists in all members of that group. This lack of knowledge of snake morphology has hampered taxonomists trying to erect a classification of the Serpentes reflecting true relationships (Dowling, 1959).

Among the previous writers on head muscles of pythonids and boids, D'Alton (1834) was the first. His account of the muscles of the head, trunk, pelvic and tail regions of *Python bivittatus* forms an excellent beginning even though he uses letters or descriptive phrases instead of names for the muscles. Owen (1866) and Bronn (1890) gave generalized discussions of snake head muscles and innervations using illustrations of *Python.* The more prominent head muscles of *Python regius* were described rather briefly by Phisalix, (1922). Lakjer (1926) included *Boa constrictor* in his extensive comparison of the adductor mandibulae and constrictores dorsales, their innervations and functions in a number of reptiles and birds. In 1935, Radovanovic compared the form of a few head muscles in a group of snakes including three boids and pythonids. The usefulness of the description of the head muscles of *Eunectes murinus* by Anthony & Serra (1950) is limited by its brevity. Haas (1955) suggested a new taxonomic position for *Loxocemus* based on musculature. Frazzetta (1959) began a series of papers on boid skulls; therefore, descriptions of skulls will be omitted here.

Materials and Methods

Five specimens of *Boa constrictor,* four from Chicago Natural History Museum (CNHM 34489, 31700, 31702, 31703) and one from the American Museum (AM 79032), were dissected with the aid of a Bausch & Lomb stereozoom dissecting microscope. A *Boa constrictor* skull, CNHM 22363, was used in determining exact locations of origins and insertions. Albright & Nelson (1959) was used in identifying the muscles but the terminology was found to be cumbersome and was abandoned in favor of Lubosch's terms (1938). The identification of nerves was accomplished with the aid of Owen (1866), Bronn (1890), Lakjer (1926) and Oelrich (1956). Hoffstetter (1939) was used for osteological terms when possible. A live specimen of *Boa constrictor,* caught in Trinidad, West Indies, in the summer of 1960, was observed while feeding, and muscle functions were deduced from these observations.

Trigeminal Innervation

Externally, the opening in the cranium for the trigeminal nerve is divided by a septum of bone into an anterior and posterior trigeminal foramen. The anterior foramen carries the ramifications of the second (maxillary) branch of the trigeminal nerve, V_2, while the posterior foramen carries the third (mandibular) branch, V_3, and several of its ramifications. The most prominent ramus issuing from the posterior foramen is the mandibular branch, itself, passing caudoventrad over the lateral face of the adductor posterior into the mandibular fossa. From the dorsal surface of the mandibular ramus, close to the foramen, a sizable ramus, the adductor profundus and posterior nerve, is given off. Lakjer (1926, P1, XXI, figs. 180 & 182) labeled this nerve "cutaneous," which is undoubtedly a mistake for all branches of the nerve ended in the muscle. The mandibular branch also has a ventral ramus, the pterygoideus nerve, lying on the medial surface of the adductor posterior. Lakjer indicates that there are rami of this nerve to the pseudotemporalis and the adductor posterior but these were not seen. Emerging from the foramen are four smaller rami of the mandibular branch lying rostro-dorsal to the mandibular branch. The four rami may be united briefly in varying combinations. The anterior ramus is the adductor superficialis nerve and the other three constitute the adductor medialis nerve. No twig of the four rami passed to the adductor profundus as is shown in Lakjer. Issuing from the foramen ventral to the adductor superficialis and medialis nerves is the pseudotemporalis nerve. It passes rostro-ventrad to the pseudotemporalis and enters the lateral surface of the muscle.

Before the mandibular branch of the trigeminal nerve, V_3, emerges from the skull, it produces two ramifications which constitute V_4. These are the retractor pterygoidei and retractor vomeris nerve and the protractor pterygoidei and levator pterygoidei nerve. There are three foramina located, in general, ventro-medial and anterior to the foramina trigemini, by which these ramifications leave the cranium. The retractor pterygoidei and retractor vomeris nerve utilizes the anterior one of the three and does not rebranch until after its emergence. The protractor pterygoidei and levator pterygoidei nerve divides into branches a. and b. which exit through the posterior foramen and the center foramen, respectively. Branch a. supplies the protractor pterygoidei while branch b. affords innervation to both the protractor and levator of the pterygoid (Lakjer, 1926).

Constrictores Dorsales

1a. Levator pterygoidei
1b. Protractor pterygoidei
1c. Retractor pterygoidei
1d. Retractor vomeris

The constrictores dorsales are the muscles of the palatal region governing movements of the visceral skeleton. A protractor quadrati is not differentiated in *Boa constrictor*.

1a. *Levator pterygoidei.*—(Synonymy: Hebemuskel des inner Flügelbeins, D'Alton, 1834; pterygo-parietalis, Bronn, 1890; Radovanovic, 1935; post-orbito-pterygoideus, Anthony & Serra, 1950). (Text-fig. 1). The levator pterygoidei is a fleshy, short muscle of the deep postorbital region. The fibers run from the parietal to the pterygoid in a ventro-caudal direction.

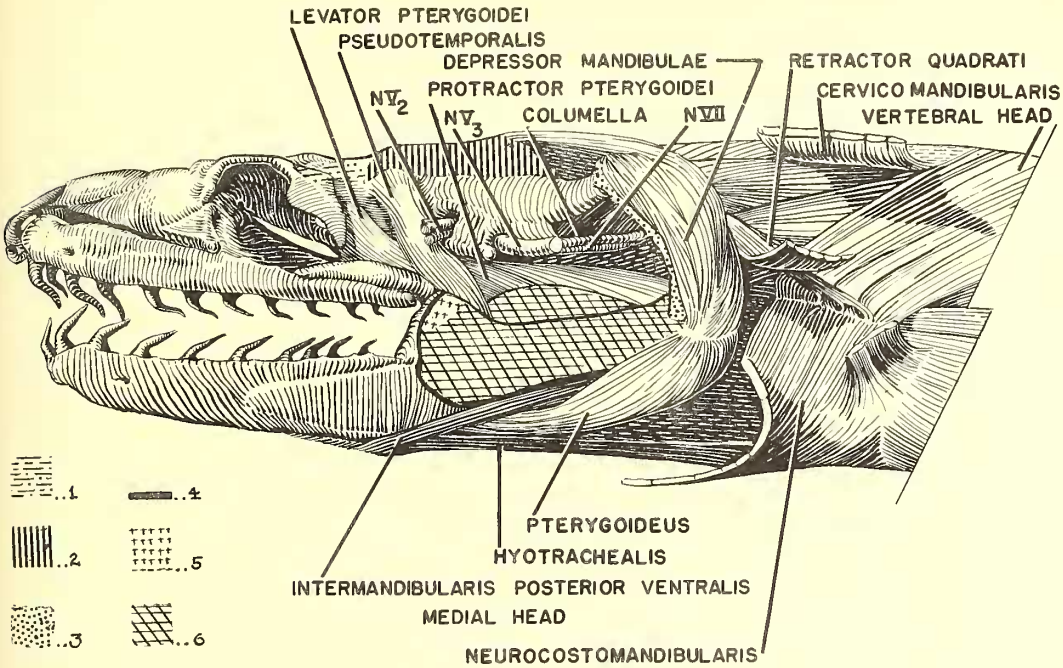
Location.—The levator pterygoidei is a deep lateral muscle lying medial to the adductores mandibulae externi and reaching anteriorly into the orbital region, where its medial surface is in contact with the retractor pterygoidei. The protractor pterygoidei lies immediately dorsal to the levator in the insertional region.

Origin.—On the ventro-posterior edge of the transverse process of the parietal and a small portion of the ventro-rostral, or orbital, face of the process.

Insertion.—On the dorsal face of the pterygoid immediately posterior to the pterygo-ectopterygoid articulation and the lateral face of the crista pterygoidea caudad to the point where the ridge becomes the lateral edge of the pterygoid.

Innervation.—Branch b. of the protractor pterygoidei and levator pterygoidei nerve leaves the cranium through the middle foramen of the V_4 foramina. Branch b. innervates the levator pterygoidei entering the muscle after sending twigs to the protractor pterygoidei.

Function.—The levator pterygoidei has a more complex activity than the mere raising of the pterygoid. The crista pterygoidea is laterally concave and has an upswinging curve to its dorsal edge, which, when the pterygoid is protracted and elevated, is pushed against the pterygoid process of the basisphenoid. The pterygoid process serves as a pivot and the ptergoid, due to the shape of the crista pterygoidea, rotates on a transverse axis at the point of contact. Thus, the levator pterygoidei, in elevating and protracting the posterior half of the pterygoid, causes the anterior area to be depressed, and in doing so, lowers the palatine process of the maxillary. The ectopterygoid is likewise depressed, lowering the posterior end of the maxillary. This action is assisted by the pterygoideus. The maxillary



TEXT-FIG. 1. Deep muscles of *Boa constrictor,* lateral view. **1.** Origin of adductor superficialis. **2.** Origin of adductor medialis. **3.** Origin of adductor profundus. **4.** Insertion of adductor superficialis. **5.** Insertion of adductor medialis. **6.** Insertion of adductor profundus and posterior.

then pivots on its palatine process, raising the anterior end.

1b. *Protractor pterygoidei.*—(Synonymy: Innerer, hinterer Flügelmuskel, D'Alton, 1834; presphenopterygoideus, Owen, 1866; pterygosphenoidalis posterior, Bronn, 1890; Radovanovic, 1935; spheno-pterygoideus, Phisalix, 1922; Anthony & Serra, 1950). (Text-fig. 1). The protractor pterygoidei is a large well-developed muscle having its ventral surface in contact with the mucosa anteriorly and with the pterygoid, posteriorly. In *Boa,* although some of the fibers insert on the quadrate, a protractor quadrati is not differentiated. From the basisphenoid, the fibers run caudo-laterad to the very end of the pterygoid, covering almost all of the dorsal surface of the pterygoid from the pterygoid process of the basisphenoid caudad. The protractor pterygoidei is fleshy throughout. Although the crista pterygoidea tends to divide the muscle into two bundles, two heads are not formed.

Location.—The protractor pterygoidei is medial to the adductores mandibulae externi. The latero-anterior fibers are in contact with the levator pterygoidei, while medially the fibers are adjacent to body muscle which have their origins on the basisphenoid and basioccipital. The anterior fibers are separated from the retractor vomeris by a heavy sheet of fascia.

Origin.—On the basisphenoid along the midventral area and the median ridge. It also extends onto the medial and postero-medial faces of the pterygoid process of the basisphenoid and onto the basioccipital in the midventral region. The level of the third pterygoid tooth socket marks the anterior end of the origin.

Insertion.—Beginning at the level of the footplate (posterior to the insertion of the levator pterygoidei), on the dorsal surface of the pterygoid. A fasiculus of the protractor pterygoidei inserts on the quadrate ventral to the process to which the columella attaches.

Innervation.—The protractor pterygoidei and levator pterygoidei nerve of V_4 divides into branches a. and b. Branch a. finds its egress through the posterior foramen of the V_4 foramina and innervates the protractor pterygoidei. Branch b. utilizes the middle foramen and innervates both the protractor and levator pterygoidei.

Function.—Protraction of the entire palatopterygoid complex, and, since the quadrate and mandible are bound tightly by ligaments to the posterior tip of the pterygoid, they also are protracted. Because of the location of the transverse

process of the premaxillary, the maxillary cannot move straight forward from a resting position. The protractor pterygoidei pulls the pterygoid mediad during protraction and this action is reflected in the posterior tip of the maxillary through the ectopterygoid. The anterior end of the maxillary is thus abducted laterad as the bone pivots at the palatine process enabling the maxillary to be protracted.

The postero-ventral projections of the prefrontals are connected to the palatine and maxillary by ligaments. These connections transmit the movements of the palato-pterygoid complex to the nasal complex and the protraction of the former causes a dorsal rotation on a transverse axis of the latter.

1c. *Retractor pterygoidei.*—(Synonymy: Innerer, vorderer Flügelmuskel, D'Alton 1834; presphenopalatine, Owen, 1866; pterygo-sphenoidalis anterior, Bronn, 1890; Radovanovic, 1935; spheno-palatinus, Phisalix, 1922; Anthony & Serra, 1950). Another muscle of the ventro-lateral parietal region, the retractor pterygoidei, is situated, for the most part, medial to the levator pterygoidei and the course of the fibers is rostro-ventrad and very slightly laterad. No tendons are formed.

Location.—In the region of its origin, the retractor pterygoidei occupies the concave antero-lateral face of the pterygoid process of the basisphenoid and the levator pterygoidei lies dorso-lateral to it. More anteriorly, the fascia of the orbit covers the dorsal surface of the retractor pterygoidei. The pterygoid and mucosa are found ventral to the muscle and the retractor vomeris, ventro-medial, the two muscles being separated by a sheet of heavy fascia. Caudally, the pterygoid process separates the retractor pterygoidei from the protractor.

Origin.—Considering the small size of the retractor pterygoidei, the origin is rather broad, occupying the area between the transverse process of the parietal and the pterygoid process of the basisphenoid, including the antero-lateral face of the latter process, and the ventro-lateral region of the parietal anterior to that process.

Insertion.—On the pterygoid, on its dorso-medial ridge, between the levels of the vomerine process of the palatine and the pterygoid process of the basisphenoid.

Innervation.—The retractor vomeris and retractor pterygoidei nerve leaves the skull through the anterior foramen of the V_4 group. The nerve divides sending a branch to the retractor vomeris and one to the retractor pterygoidei.

Function.—The protraction of the pterygoid complex is accompanied by a slight depression of the anterior end of the pterygoid and the posterior end of the palatine plus some lateral displacement of this part of the complex. The retractor pterygoidei retracts the pterygoid complex, elevates the anterior end of the pterygoid and counteracts the lateral displacement.

1d. *Retractor vomeris.*—(Synonymy: Zurückzieher des Vomer, D'Alton, 1834; presphenovomerine, Owen, 1866; vomero-sphenoideus, Bronn, 1890; spheno-vomerinus, Phisalix, 1922; spheno-vomeris, Anthony & Serra, 1950). The retractor vomeris is a palatal muscle lying parallel to the mid-ventral line of the cranium. This muscle is comprised of a fleshy posterior and a tendinous anterior portion. At the origin, the muscle is compressed dorso-laterally and ventro-medially so that it lies in a plane tilted about 45 degrees from the sagittal plane of the head. The fibers run rostrad, converging somewhat from the origin to the tendon.

Location.—At its origin, the retractor vomeris is compressed between the retractor pterygoidei, dorso-laterally, and the protractor pterygoidei, ventro-medially. Anterior to the origin, the mucosa covers the muscle ventrally and fascia enclosing Meckel's cartilage is dorsal to it.

Origin.—From the sharp anterior ridge of the pterygoid process of the basisphenoid and a small area of the wall of the process just lateral to the ridge.

Insertion.—The prominent tendon of the retractor vomeris inserts on the posterior point of the lamellar process of the vomer.

Innervation.—By a twig of the retractor vomeris and retractor pterygoidei nerve.

Function.—The elevation of the nasal complex, which includes the paired vomers, is opposed by the action of the retractor vomeris.

Adductores Mandibulae

2a. Adductor mandibulae externus superficialis

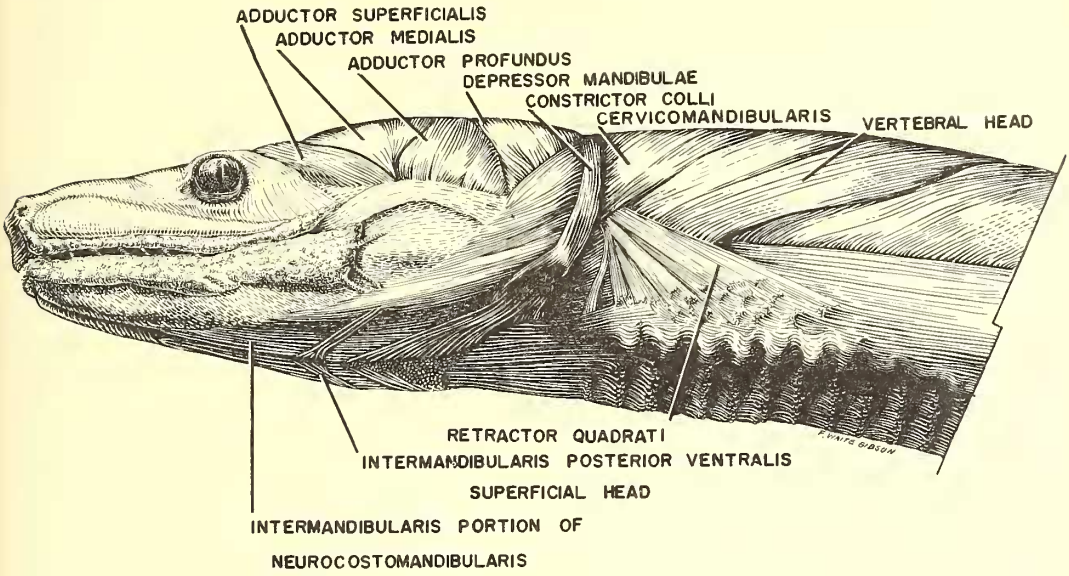
2b. Adductor mandibulae externus medialis

2c. Adductor mandibulae externus profundus and adductor mandibulae posterior

2d. Adductor mandibulae internus pterygoideus

2e. Adductor mandibulae internus temporalis (pseudotemporalis)

The adductores mandibulae, the largest group of head muscles, form the contours of the head in the parietal region, from the parietal crest to the mandible and from the postorbital to the quadrato-mandibular articulation. They are important in controlling the rotation of the mandible on a longitudinal axis, as well as the closing



TEXT-FIG. 2. Superficial muscles of *Boa constrictor,* lateral view.

of the lower jaw. The adductor superficialis initiates the closing action, and, because of the position of the insertion of the aponeurosis, also rotates the teeth inward. The pterygoideus, by contracting slightly in conjunction with the depressor mandibulae, rotates the teeth outward during the opening of the mouth.

The adductor profundus and adductor posterior are separated in the area of the mandibular branch of the trigeminal nerve only and are treated together here.

The pterygoideus is not subdivided.

2a. *Adductor mandibulae externus superficialis.*—(Synonymy: temporalis a, D'Alton, 1834; masseter, Owen, 1866; Radovanovic, 1935; parietali-quadrato-mandibularis a, Bronn, 1890; temporalis anterior, Phisalix, 1922; Anthony & Serra, 1950). (Text-fig. 2). This muscle lies posterior to the orbital region but anterior to the other two adductor externus muscles. The fibers are directed caudo-laterad from the origin and curve caudo-ventrad around the side of the head, forming a band. The fleshy part of the muscle lies in a depression of the adductor medialis and is superficial except where the muscle becomes aponeurotic. There it is medial to the rictal plate and zygomatic ligament. A sheet of fascia extends from the medial surface of the rictal plate and at right angles to it, upward to the superficial part of the adductor medialis, becoming continuous with the fascia of the muscle. This sheet of fascia separates the adductor superficialis from the medialis.

Location.—A superficial muscle but its aponeurosis is covered by the zygomatic ligament and the rictal plate. The muscle lies in a depression of the adductor medialis and only the anterior end is in contact with the underlying transverse process of the parietal.

Origin.—(Text-fig. 1). From the dorso-caudal faces of the parietal, transverse process, and the postorbital, just posterior to the fronto-parietal suture.

Insertion.— (Text-fig. 1). The extensive aponeurosis by which the adductor superficialis is inserted also receives a portion of the adductor medialis. The aponeurosis is attached to the mandible, from the anterior edge of the coronoid process, ventrad along the lateral face of the angular passing just posterior to the supra-angular foramen, and caudad along the crista lateralis to terminate anterior to the sigmoid fossa.

Innervation.—The adductor superficialis nerve, which branches off the anterior ramus of the adductor medialis nerve before emerging from the posterior trigeminal foramen, enters the adductor superficialis on its medial surface.

Function.—When the mandible is fully abducted, both ventrad and laterad, and rotated laterad on its longitudinal axis, contraction of the adductor superficialis rotates the teeth inward and adducts the mandible dorsad.

2b. *Adductor mandibulae externus medialis.*—(Synonymy: temporalis b, D'Alton, 1834; temporalis, Owen, 1866; parietali-quadrato-mandibularis b, Bronn, 1890; temporalis medialis,

Radovanovic, 1935; Anthony & Serra, 1950). (Text-fig. 2). This bulky muscle is the largest of the three adductor externus muscles. The fibers, converging ventrad, caudo-ventrad, and rostro-ventrad, from a very wide origin, insert both on the bone of the mandible and on an aponeurosis. Part of the aponeurosis is continuous with that of the adductor superficialis. There is some indication of the development of two fasciculi in the region of the insertion. Here the aponeurosis is also separate, forming two layers which soon fuse.

In the posterior portion of the adductor medialis, there is fusion of several small caudo-medial fasciculi with the adductor profundus. Some specimens exhibit slight fusion between the adductor superficialis and medialis.

Location.—Dorsally, the adductor medialis lies between the adductor superficialis and profundus and, in this area, it is superficial and quite prominent. In the postorbital region, the adductor superficialis crosses over the medialis. Caudo-dorsally, the occipital slip of the depressor mandibulae crosses a portion of the adductor medialis. The large postero-ventral face of the muscle adjoins the adductor profundus and posterior. Medially, the muscle overlies the lateral face of the pseudotemporalis, the crest of the parietal, the supratemporal, supraoccipital, maxillary branch of the trigeminal nerve, and the levator pterygoideus.

Origin.—(Text-fig. 1). Covering the entire face of the parietal and supraoccipital crest. Most of the fibers pass over the dorso-lateral face of the supratemporal, forming only a loose attachment with the periosteum. Near the quadrato-supratemporal articulation, some fibers originate from the supratemporal, ventro-lateral, to dorso-medial surfaces, and from a small portion of the fascia of the depressor mandibulae. At the posterior extremity of the origin, some of the fibers, coming from the exoccipital and a tendon from the ventro-medial face of the supratemporal, pass dorso-rostrad over the supratemporal and thence ventro-rostrad to the insertion.

Insertion.—(Text-fig. 1). Either by fibers directly to the bone of the dorsal tip of the coronoid process or by tendon and fibers with the fibrous portion confined to the caudo-lateral face of the process. The greater part of the insertion of the adductor medialis is aponeurotic. The aponeurosis is actually a medial layer of the adductor superficialis aponeurosis and the two fuse ventrally at the rostral end of the insertion which runs from the coronoid process ventrad over the lateral face of the supra-angular and on to the crista lateralis.

Innervation.—The adductor medialis nerve is comprised of three rami of V_3 emerging from the antero-dorsal part of the posterior trigeminal foramen. The anterior ramus of the three gives rise to the adductor superficialis nerve. The nerves enter the medial surface of the muscle.

Function.—The fibers, straightened into a ventro-lateral direction by the abduction and protraction of the mandible, adduct the mandible and rotate it mediad by their contraction.

Variations.—The fibers originating from the exoccipital and the tendon from the ventro-medial face of the supratemporal and the fascia of the depressor mandibulae may be either a part of the adductor medialis or a part of the adductor profundus.

Along the caudal border of the adductor medialis, a shallow separation into two fasciculi with a corresponding doubling of the aponeurosis is sometimes discernible.

While the coalescence of the adductor medialis with the superficialis is most often absent and, when present, involves only a few fibers, fibers common to both adductor medialis and profundus are nearly always present and may prevent a clear-cut division of the muscles for half of their adjoining surfaces.

2c. *Adductor mandibulae externus profundus and adductor mandibulae posterior.*—(Synonymy: temporalis c, D'Alton, 1834; posttemporalis, Owen, 1866; parietali-quadrato-mandibularis c and d, Bronn, 1890; temporalis posterior, Phisalix, 1922; Radovanovic, 1935; Anthony & Serra, 1950). (Text-fig. 2). This is also a massive muscle which lies, principally, caudo-ventral to the adductor medialis, filling the angle formed by the quadrate and the mandible. The direction of the fibers varies from ventrad to rostro-ventrad. The mandibular branch of the trigeminal nerve provides a demarkation of the adductor profundus and posterior. The adductor posterior does not form two heads.

A tendon originating from a lateral tuberosity of the head of the quadrate, extends ventrad into the muscle. Fibers of the muscle originate from this structure on both its rostral and caudal faces. The fibers from the rostral face pass rostro-ventrad while those from the caudal face are directed caudo-ventrad.

Location.—The adductor profundus and posterior occupies the right angle formed by the quadrate and the mandible. It is in contact dorsally and anteriorly with the medialis, dorso-caudally and posteriorly with the depressor mandibulae and the quadrate, ventrally with the mandible and the pterygoideus. The dorsal half of the muscle is superficial, but the ventral por-

tion is covered by the aponeurosis of the adductor superficialis, the zygomatic ligament, and the cervicomandibularis - neurocostomandibularis aponeurosis.

Origin.—(Text-fig. 1). The entire rostro-medial face of the quadrate, along with all surfaces of the free distal end of the supratemporal and fascia of the depressor mandibulae in the region of the quadrato-supratemporal articulation. The tendon from the quadrate also provides for attachment of fibers.

Insertion.—(Text-fig. 1). The lower boundary of the insertion of the adductor profundus follows the insertion of the adductor superficialis and medialis, being posterior to the medialis in the region of the coronoid process and dorsal to the aponeurosis along the crista lateralis. The adductor profundus inserts on the lateral face of the supra-angular from the quadrato-mandibular articulation forward to these limits.

Innervation.—A ramus emerging from the dorsal surface of V_3 passes over the lateral surface of the adductor posterior and sends twigs to both adductor profundus and posterior.

Function.—Adducts the mandible, particularly in setting the teeth firmly into the prey.

Variations.—The group of fibers from the tendon on the ventro-medial face of the distal end of the supratemporal may either pass ventral to that bone and thence rostro-ventrad, or they may pass dorsal to the bone. In the former case the fibers are a part of the adductor profundus and in the latter case they form a part of the adductor medialis.

Other variations are described in conjunction with adductor medialis.

2d. *Adductor mandibulae internus pterygoideus.*—(Synonymy: Ausserer Flügelmuskel, D'Alton, 1834; transverso-maxillo-pterygo-mandibularis, Bronn, 1890). (Text-fig. 1). The pterygoideus is a fleshy, deep-bellied muscle situated medial to the proximal end of the mandible. Although its fibers converge rostrally from the origin on the retroarticular process, they do not form a tendon. A subdivision, pterygoideus accessorius, was not found, nor was there any insertion of fibers onto the mucosa of the mouth.

Location.—The pterygoideus covers the posterior half of the ventral surface of the pterygoid bone. The anterior two-thirds of the ventral surface of the pterygoideus is covered by the mucosa of the mouth and throat, while the posterior third is in contact with the neurocostomandibularis. The dorsal surface is adjacent to the mandible, the pterygoid and the adductor posterior.

Origin.—From the ventral surface of the posterior tip of the ectopterygoid, caudad, covering the ventral face of the pterygoid except for the medial margin.

Insertion.—On the retroarticular process and the lateral, ventral and medial surfaces of the compound bone of the mandible below the sigmoid fossa.

Innervation.—V_3, before emerging from the foramen, gives off from its ventral surface the fair-sized pterygoideus nerve which passes mediad and ventro-caudad on the medial face of the adductor posterior to the pterygoideus muscle.

Function.—This muscle during abduction causes a lateral movement of the distal end of the mandible and a lateral rotation on the longitudinal axis. At the same time, during protraction of the pterygoid complex, contraction of the pterygoideus depresses the ectopterygoid which in turn depresses the posterior end of the maxillary. This rotates the maxillary on a transverse axis in the region of the palatine process, elevating the anterior end of the maxillary.

The pterygoideus assists in closing the mouth and, working with the adductor profundus, exercises a fine control of the rotation of the mandible.

2e. *Adductor mandibulae internus temporalis* (pseudotemporalis).—(Synonymy; temporalis d, D'Alton, 1834; parieto-mandibularis profundus, Phisalix, 1922; temporalis anterior, Radovanovic, 1935; parieto-mandibular, Anthony & Serra, 1950). (Text-fig. 1). A deep adductor of the mandible lying between the adductor medialis and the parietal and separated from the medialis by the maxillary branch of the trigeminal nerve, V_2. It is generally strap-shaped with a slight fanning out of the fibers at their origin. The direction of the fibers is ventro-caudal.

Location.—Adjacent to the parietal and constrictores dorsales medially and the adductor medialis, laterally, the pseudotemporalis stretches from the anterior part of the lateral face of the parietal to the coronoid process.

Origin.—From the lateral face of the parietal immediately below the parietal crest lying between the origin of the adductor superficialis anteriorly and the supratemporal, posteriorly.

Insertion.—On median plane of the coronoid process and the anterior edge of the median lamella of the mandibular fossa. There is no fibrous insertion on the rictal plate, but the fascia of the pseudotemporalis (anterior edge) is continuous with the median fold of the rictal plate.

Innervation.—A single pseudotemporalis nerve leaves the cranium via the posterior trigeminal foramen ventral to the adductor superficialis and medialis rami and passes rostro-ventrad, re-

dividing and entering the lateral face of the muscle. No pseudotemporalis ramus of the pterygoideus nerve was present.

Function.—An adductor of the mandible.

Variation.—The fanning-out of the fibers at their origin may be absent.

Constrictores Ventrales

3a. Intermandibularis anterior

3b. Intermandibularis posterior dorsalis

3c. Intermandibularis posterior ventralis

The three muscles in the floor of the mouth which are innervated by the mandibular branch of the trigeminus, V_3, are classified as the constrictores ventrales. They are, generally, long, thin muscles with subdivisions into various heads. They adduct the mandibles towards the midventral line and constrict and elevate the floor of the mouth after it has been stretched during the deglutition.

A pair of aponeuroses, lateral to the midventral line, separate the intermandibular muscles of the right and left sides from each other and from the skin of the area. The aponeuroses stretch from the anterior tip of the mandibles back to the insertion of the intermandibularis anterior. Laterally, they become coalesced with the aponeurosis of the neurocostomandibularis. This arrangement permits a wide range of independent action between the two mandibles.

Innervation of the constrictores ventrales is by means of the inferior dentary nerve, which is a branch of the mandibular ramus of the trigeminal nerve (Hoffstetter, 1939). The inferior dentary nerve enters the mandibular canal through the Meckelian foramen located within the manibular fossa. This nerve, joined by the chorda tympani which has entered the canal by way of the retroarticular foramen, courses anteriorly along with Meckel's cartilage. Several sensory branches leave the inferior dentary nerve through various foramina, including the foramen in the angular, before the main root reaches the splenial, where a foramen and the beginning of the Meckelian sulcus are located. The foramen, which is ventral to the sulcus, provides the exit for a motor ramus of the inferior dentary nerve. The ramus, if named according to Lakjer's method, would be the intermandibularis-cutaneous nerve. It sends ramifications to the intermandibularis anterior and posterior, dorsalis and ventralis and to the skin.

3a. *Intermandibularis anterior.*—(Synonymy: Die sich kreuzenden Muskeln des Unterkiefers, D'Alton, 1834; intermaxillaris, Bronn, 1890). The intermandibularis anterior extends from the distal tip of the dentary caudad for about two-thirds of the length of that bone. The fibers run caudo-mediad, none directly mediad. There are two heads separated at their origin by the origin of the genioglossus. These fairly heavy bands of muscle remain distinct except at the insertion.

The connective tissue of the midventral line at the insertion of the intermandibularis anterior is continuous with a median vertical sheet of fascia. The dorsal end of the sheet attaches to the floor of the mouth ventral to the tongue and ends anteriorly at the point where the tongue is protruded from its sheath. Thus the intermandibularis anterior has a connection with the tongue sheath.

No fasciculus which inserts on the mandibular gland (pars glandularis, Albright & Nelson, 1959) is formed.

Location.—Most of the ventral surface of the intermandibularis is covered by the aponeurosis of the neurocostomandibularis; only the insertion is entirely superficial and, even in this area, a small part is medial to one head of the intermandibularis posterior ventralis. The dorsal face of the intermandibularis anterior is adjacent to the genioglossus, geniotrachealis and the intermandibularis posterior dorsalis.

Origin.—The origins of the two heads of the intermandibularis anterior, which are on the ventro-medial surface of the curved distal tip of the mandible, are separated by the origin of the genioglossus.

Insertion.—On fascia of the midventral line, between the levels of the anterior mylohyoid foramen and the splenio-angular suture.

Innervation. — The intermandibularis-cutaneous branch of the inferior dentary nerve leaves the mandibular canal through the foramen in the splenial, directed ventro-mediad, sending a branch to the intermandibularis posterior ventralis and the skin before dividing into two approximately equal rami. The anterior ramus turns rostrad to send twigs into the dorso-lateral and ventral faces of the intermandibularis anterior and into the dorsal surface of the intermandibularis posterior dorsalis.

Function.—Adduction of laterally displaced distal tips of the mandibular rami, contraction of the floor of the mouth, or protraction of the tongue sheath and/or larynx depending on interaction with other muscles.

Variations.—Some fibers may originate on the aponeurosis of the neurocostomandibularis. There may be much interlacing of fibers at the insertion with the intermandibularis posterior ventralis.

3b. *Intermandibularis posterior dorsalis.*—It is partially embedded in loose connective tissue, making dissection tedious. It is a better developed and apparently more specialized muscle than the other constrictores ventrales. The two heads, glandular and mucosa, are equal in diameter. The fibers, originating on the midventral line dorsal to the intermandibularis anterior, proceed rostro-laterad to the mandible. There they turn rostro-medial and insert on the caudal end of the mandibular gland and the mucosa dorsal and caudal to the gland. The fibers at the insertion of the mucosa head fan out and form a cup-like depression around the dorsal and dorso-caudal portion of the gland. The intermandibularis posterior dorsalis, along with the geniotrachealis, makes an almost complete muscular encasement for the mandibular gland.

Location.—This is a deep muscle of the anterior intermandibular region. Due to the curving course of the intermandibularis posterior dorsalis, this muscle lies ventral to the geniotrachealis and genioglossus at its origin and dorsal to them at its insertion. The fibers inserting on the dorsal-lateral area of the mandibular gland are covered by a glandular fasciculus from the geniotrachealis. The medial fibers of the mucosa head insert quite close to fibers from the anterior segment of the geniotrachealis. Since the fibers of both muscles are embedded in connective tissue, it is difficult to separate them but no fusion was found.

Origin.—On the connective tissue of the midventral line dorsal to the intermandibularis anterior.

Insertion.—Insertion of the mucosa head is on an extensive area of the mucosa caudal and dorsal to the mandibular gland from the level of the anterior tip of the splenial rostrad over the caudal one-third of the gland. The glandular head inserts on the caudal tip of the gland and the postero-lateral third of the glandular sheath.

Innervation.—The inferior dentary nerve gives off an intermandibularis-cutaneous ramus through the foramen in the splenial which, after branching to the intermandibularis posterior ventralis and intermandibular skin, bifrucates. The anterior bifrucation sends twigs rostrally and medially into the dorsal surface of the intermandibularis posterior dorsalis and into the intermandibularis anterior.

Function.—The reason for such a sizable muscle of this particular arrangement is not immediately clear. Obviously, its action would oppose that of the intermandibularis anterior and glandular fasciculus of the geniotrachealis when these two muscles are used to protrude and elevate the tongue sheath and larynx. Also the intermandibularis posterior dorsalis constricts the mandibular gland, but it would seem that both of these actions could be accomplished by a much smaller muscle unless the contents of the gland are forcibly extruded.

Variations.—The fibers at the origin of the intermandibularis posterior dorsalis may interdigitate with those from the intermandibularis posterior ventralis which insert in the same area.

3c. *Intermandibularis posterior ventralis.* —(Synonymy: Die sich kreuzenden Muskeln des Unterkiefers, D'Alton, 1834; intermandibularis posterior, Owen, 1866; Phisalix, 1922; Anthony & Serra, 1950; intermaxillaris, Bonn, 1890). (Text-figs. 1 & 2). The intermandibularis posterior ventralis is comprised of three extremely long, thin, completely separated heads with fibers directed rostro-mediad from the medial surface of the proximal end of the mandible to the midventral line. The superficial head is only 1½ mm. wide and, since it is buried in the loose connective tissue between the skin and the neurocostomandibularis, almost impossible to find. The medial and lateral heads are medial to the neurocostomandibularis and are much larger. The medial and lateral heads are flattened vertically at their origins.

Location.—This muscle is found in the floor of the mouth from the proximal region of the mandible anterior for two-thirds the length of the bone. The superficial head of the intermandibularis posterior ventralis is ventral to the neurocostomandibularis, while the medial and lateral heads are dorsal to it except at their insertions, where they also become superficial. At their origin, the two main elements are situated between the mandible and the pterygoideus.

Origin.—The origins of the main elements of the intermandibularis posterior ventralis are taken from the medial surface of the mandible, the lateral head from the ventro-medial face of the supra-angular just posterior to the caudal tip of the angular, and the medial head posterior to this and dorsal to the crista lateralis which in this area forms a ventral ridge. Both origins lie in an antero-dorsal, caudo-ventral line, the posterior one curving slightly upward. The superficial head originates from the aponeurosis of the cervicomandibularis near the antero-ventral tip of the fibers.

Insertion.—On a superficial pad of loose connective tissue on the midventral line anterior to the hyoid apparatus beginning posteriorly at the level of the splenial-angular suture and reaching the level of the foremost tip of the splenial anteriorly.

Innervation.—From the inferior dentary nerve, the intermandibularis-cutaneous ramus proceeds from the mandibular canal by way of the foramen in the splenial, ventro-medially. The first branch, given off close to the foramen, sends a twig caudally along the latero-dorsal edge of the intermandibularis posterior ventralis innervating the muscle. The other twigs from this branch continue medially, then turn ventrally to innervate the skin.

Function.—The superficial head appears to be much too weak to assist in the swallowing action and probably only helps to constrict the skin after the swallowing has been completed. The main elements of the muscle, however, by contracting after the prey has passed their insertion, constrict the throat, preventing the food from being pushed back out the mouth as the rib region is brought forward. The possibility of such actions as the retraction of the tongue sheath and larynx and the protrusion and adduction (toward the midventral line) of the proximal end of the mandible seem unlikely because the amount of loose connective tissue at the insertion does not give the muscle firm anchorage.

Variations.—The medial and lateral heads may be fused at their origin, having a common origin which may be ventro-lateral on the crista lateralis rather than ventro-medial. The insertional fibers may interlace with intermandibularis anterior and intermandibularis posterior dorsalis. A few fibers of the medial head may originate on the fascia of the pterygoideus.

Hyoid Musculature

4a. Depressor mandibulae

4b. Cervicomandibularis

4c. Constrictor colli

These three muscles are placed in this category not because of any direct connection with the hyoid apparatus but because they are innervated by the facial nerve and hence may be homologous to hyoid musculature in lower animals (Albright & Nelson, 1959). Egress for the facial nerve is by way of the facial foramen in the floor of the posterior trigeminal foramen. The palatine ramus arises close to the point of exit and passes anteriorly ventro-mediad to the Vidian canal. The facial nerve continues generally caudo-laterad, medial to the columella, to the ventro-medial surface of the depressor mandibulae. About the middle of the columella, the facial receives a ramus communicans from the petrosal ganglion of the glossopharyngeal nerve. Near the posterior end of the columella, the facial divides into three approximately equal branches: the ventro-lateral chorda tympani which enters a tiny foramen in the retroarticular process and passes forward into the mandibular canal; the middle ramus, cervicomandibularis and constrictor colli nerve; and the dorso-medial ramus, depressor mandibulae nerve.

The hyoid muscles are located, mainly, posterior to the quadrate from the mid-dorsal line to the quadrato-mandibular articulation. The constrictor colli, however, reaches ventrally around the throat to the midventral line anterior to the quadrato-mandibular articulation.

The constrictor colli is entirely superficial, as is most of the cervicomandibularis. The depressor mandibulae lies medial to the cervicomandibularis except for its dorsal area.

The depressor mandibulae and cervicomandibularis act as depressors of the lower jaw and the constrictor colli contracts the throat region.

4a. *Depressor mandibulae.* — (Synonymy: Niederzieher des Unterkiefers, D'Alton, 1834; tympanico-mandibularis, Owen, 1866; occipito-quadrato-mandibularis, Bronn, 1890; digastricus, Phisalix, 1922; Radovanovic, 1935; Anthony & Serra, 1950). (Text-figs. 1 & 2). The depressor mandibulae is a well developed muscle posterior to the quadrate. A strong slip extends dorsad forming an occipital head, distinct from the quadrate head down to the insertion. There is a dorsal extension of the fascia of the quadrato-mandibular articulation to which the occipital head attaches. The sheet of fascia presents a rostro-lateral and a caudo-medial face. Fibers from the quadrate head insert on both faces of the fascia.

The dorsal portion of the occipital head is directed caudo-laterad and the remainder, ventro-laterad. The quadrate head is directed ventro-laterad and its fibers completely surround the tendon of the retractor quadrati.

Location.—The depressor mandibulae lies beneath the constrictor colli and the cervicomandibularis with only the dorsal portion being superficial. The occipital head reaches rostro-medially between the cranial insertion of the spinalis-semispinalis and the more posterior portions of the adductor medialis. The quadrate head adjoins the adductor profundus anteriorly and the retractor costae biceps posteriorly. The retractor quadrati emerges from its origin on the quadrate from between the fibers of the quadrate head.

Origin.—The occipital head originates from the posterior fifth of the parietal crest. The quadrate head originates from a wide area on the posterior quarter of the supratemporal and the upper three-fourths of the caudo-lateral face of the quadrate.

Insertion.—On the lateral and caudo-dorsal

faces of the retroarticular process and on the sheet of fascia, which is a dorsal extension of the quadrato-mandibular articulation capsule. The insertion of the occipital head is on the dorsal lateral edge of the fascia.

Innervation.—Three rami of the facial nerve are located on the ventro-medial face of the depressor mandibulae just dorsal to the posterior tip of the pterygoid. The dorsal ramus is the depressor mandibulae nerve and it penetrates the muscle in this region.

Function.—The depressor mandibulae lowers the mandible and the occipital head pulls the distal end of the quadrate outward from the midline of the body, displacing the mandible laterad.

Variations.—The occipital head may be tendinous at its origin, in which case the origin is moved forward on the parietal crest to about the level of the anterior border of the supratemporal.

4b. *Cervicomandibularis.*—(Synonymy: Nackenunterkiefermuskel, D'Alton, 1834; trachelomastoideus, Owen, 1866). (Text-fig. 2). The cervicomandibularis, a heavy sheet of superficial muscle, medial to the constrictor colli only, is located in the lateral cervical region anterior to the neurocostomandibularis and posterior to the quadrate. It is equal in size to the vertebral head of the neurocostomandibularis. The fibers are directed from a mid-dorsal aponeurosis rostroventrad to the mandible. The aponeurosis by which the cervicomandibularis originates and inserts are both continuous with those of the neurocostomandibularis. Also, some of the fibers of the two muscles fuse.

The aponeurosis of the insertion of the cervicomandibularis is quite large, bounded by the mid-dorsal line above and the neurocostomandibularis below. It is superficial to and separate from the fascia and aponeurosis of the adductor externus muscles and the depressor mandibulae. Anteriorly it attaches to the parietal, postorbital and rictal plate. Medial to the zygomatic ligament, the aponeurosis passes ventrad over the aponeurosis of the adductor externus muscles to become confluent with the aponeurosis of the neurocostomandibularis. At the inferior labial gland, the aponeurosis has two layers, forming a pocket in which the gland lies; the lateral layer attaches to the skin lateral to the gland, and the medial layer to the dentary. Anterior to the gland, the aponeurosis is again a single layer and attaches to the dentary. It grows firmly to the posterior tip of the gland and to the skin at the angle of the mouth ventral to the rictal plate.

The dorsal part of the aponeurosis is much thinner than the tougher portion found ventral to the zygomatic ligament.

Four distinct heads of the cervicomandibularis insert on this aponeurosis; three principal ones, of almost equal size, lying in a dorsoventral plane, are here designated as dorsal, middle and ventral heads. At the point of attachment of the zygomatic ligament to the quadrato-mandibular articulation, the middle head overlies the ventral part of the dorsal head. Also in this area, the middle head gives rise to a much smaller and shorter medial head which attaches to the capsule of the quadrato-mandibular articulation.

Location.—Radovanovic's (1935) method of distinguishing the border between the cervicomandibularis and the vertebral head of the neurocostomandibularis by using the emergence of the retractor quadrati as a demarkation has been followed here, in spite of the fact that there is fusion of fibers of the two muscles dorsally.

The medial surface of the cervicomandibularis is adjacent to portions of the adductor profundus, depressor mandibulae, retractor quadrati, pterygoideus and trunk muscles.

Origin.—From the tough aponeurosis of the mid-dorsal area and the fascia of the spinalis-semispinalis muscle group. The origin begins anteriorly at approximately the level of the neural crest of the fourth vertebra and reaches posteriorly to the level of the ninth vertebra.

Insertion.—The dorsal head of the cervicomandibularis inserts on the aponeurosis dorsal to the attachment of the zygomatic ligament and on the ligament, itself, as well as the capsule of the quadrato-mandibular articulation. The middle head has an aponeurotic insertion only, and the part of the aponeurosis to which the dorsal fibers of the middle head attach is lateral to the attachment and posterior end of the zygomatic ligament. The subsidiary, medial head inserts on the quadrato-mandibular articulation posterior to the attachment of the ligament.

The ventral head has its insertion on the aponeurosis adjacent to the vertebral head of the neurocostomandibularis. The ventral head does not overlap the middle head.

Innervation.—Of the three rami of the facial nerve found on the ventro-medial face of the depressor mandibulae, the middle one is the cervicomandibularis-constrictor colli nerve. The cervicomandibularis-constrictor colli nerve branches, the dorsal branch innervating the cervicomandibularis, while the ventral branch continues through this muscle into the constrictor colli.

Function.—Contraction of the middle and ventral heads augments the neurocostomandibularis in depressing the mandibles and in swinging the distal end of the mandibles outward. The

dorsal head, by means of the insertion on the quadrato-mandibular articulation capsule, retracts the quadrate and, thus, the entire palato-maxillary complex as well as the mandible.

Variations.—The medial head may insert partially with the dorsal head on the quadrato-mandibular articulation and partially with the middle head on the aponeurosis.

4c. *Constrictor colli.*—(Synonymy: Rückwärtzieher des Zungenbeins, D'Alton, 1834; atlanto-epistropheo-hyoideus, Bronn, 1890; intermandibularis superficialis, Anthony & Serra, 1950). (Text-fig. 2). The constrictor colli is a thin, narrow band of superficial muscle. It curves from the mid-dorsal region, around the angle of the jaw to the midventral area. Thus the fibers are oriented caudo-laterad dorsally and rostro-mediad ventrally. The muscle is embedded in the loose connective tissue beneath the skin and is difficult to discern.

The fibers diverge in the throat region so that the insertion is approximately ten times broader than the origin.

Location.—The constrictor colli overlies portions of the depressor mandibulae, cervicomandibularis and neurocostomandibularis.

Origin.—From the aponeurosis of the mid-dorsal line overlying the spinalis-semispinalis muscles and the deeper fascia with which the aponeurosis is continuous, between the depressor mandibulae and the cervicomandibularis. The fibers do not extend to the mid-dorsal line.

Insertion.—On fascia near the midventral line and on the dense fibrous connective tissue shield found at the level of the larynx.

Innervation.—The ventral branch of the cervicomandibularis-constrictor colli nerve passes through the fibers of the cervicomandibularis muscle and piercing the medial surface of the constrictor colli slightly medial and caudo-dorsal to the retroarticular process, innervates that muscle.

Function.—The constrictor colli may not be as weak and ineffectual as has been supposed. Because it is attached to inelastic tissues at its origin and half of its insertion, its action must be one of constriction. The throat, enlarged by the passage of food, would not offer any resistance to this action and so a large muscle would not be necessary. The constriction of the skin in the area is secondary since the muscle is attached to the skin by loose connective tissue only, except for part of the insertion. The constriction action is also used during the swallowing process. When the throat has been enlarged and the floor of the buccal cavity and anterior end of the oesophagus displaced caudally by the passage of food, then the constrictor colli, retractor quadrati and intermandibular portion of the neurocostomandibularis pull the skin forward over the prey, spreading the two segments of the hyoid apparatus laterad and dorsad.

Hypobranchial-spinal Musculature

5a. Hyoglossus
5b. Hyotrachealis
5c. Genioglossus
5d. Geniotrachealis
5e. Neurocostomandibularis
5f. Retractor quadrati

These muscles, grouped according to Albright & Nelson (1959), include those innervated by the glossopharyngeal, vagus, accessorius, hypoglossal and the first spinal nerves. Here, the muscles of the neck region not concerned with deglutition have been omitted. The innervation, due to much mixing of fibers, is confusing and has not been satisfactorily worked out.

All muscles of this group are flat, either fan-shaped or bands. They are located in the lateral cervical region posterior to the quadrate, and the throat and intermandibular regions.

The four extrinsic muscles of the tongue and larynx move those organs while the neurocostomandibularis abducts the mandible and the retractor quadrati acts on the hyoid and the skin.

The pathways of the glossopharyngeal, accessorio-vagus, hypoglossal, and first and second spinal nerves, and the lateral superficial cervical trunk (sympathetic) are so interwoven and in many places confluent, that it is necessary to describe all of them in order to make clear which nerve is being discussed. The identification of these nerves was accomplished through the use of Owen (1866), Bronn (1890), Hoffstetter (1939) and Oelrich (1956). Oelrich has described the nerves of *Ctenosaura* in more detail than the other author, and where the nerves of *Boa* have had a distribution closely following that of *Ctenosaura,* it has been assumed that the nerves were made up of the same components as those of *Ctenosaura.* It is realized, of course, that this is a shaky basis for such an assumption but, lacking a microscopic study of the nerves, the best that can be done. Bronn (1890, p. 1486) states that the Xth and XIth cranial nerves are always fused in snakes, so all references to the vagus herein will mean the combined accessorio-vagus.

The glossopharyngeal and vagus nerves, bound together by a connective tissue sheath, emerge from the skull through the jugular foramen in the exoccipital. The glossopharyngeal nerve itself is small, but here it is accompanied

by many sympathetic fibers so that it is as large as the vagus. The glossopharyngeal nerve, dorsal to the vagus at the jugular foramen, enlarges into the petrosal ganglion not far from the skull. At the ganglion, the vagus lies medial to the glossopharyngeal and the two nerves become fused in the posterior part of the ganglion. Dorsally the petrosal ganglion has two rami communicating with the facial nerve; an antero-medial one to the chorda tympani in the region of the columella, and one which goes antero-ventrally over the lateral face of the ganglion to join the palatine ramus of the facial. The hypoglossal nerve issues from the skull via three small foramina in the exoccipital which are connected by canals within the bone. Outside the skull, the rami of the hypoglossal fuse and receive fibers from the first two spinal nerves. The deep cervical sympathetic trunk, which connects the spinal nerves close to the vertebrae, sends a terminal ramus from the first spinal nerve antero-laterad to the vagus quite near the jugular foramen. The terminal ramus is joined by a communicating ramus from the hypoglossal before entering the vagus. At this locus, the vagus has a communicating ramus with the glossopharyngeal and another with the hypoglossal. The combined hypoglosso-spinal nerve coalesces with the vagus posterior to the petrosal ganglion. Posteriorly from the ganglion issue three main nerve roots which may be fused for a short distance.

The three roots, the glossopharyngeo-vagal, the vago-hypoglosso-spinal, and the vago-sympathetic, proceed caudo-laterally and slightly ventrally to the region of the posterior tip of the pterygoid, where they swing more ventrad to the mandibular area. The lateral superficial cervical trunk, which is the sympathetic part of the vago-sympathetic root, turns caudad between the carotid artery and the jugular vein, the vagal part of the root having previously separated from the root and gone to the pharynx and trachea. The other roots, the glossopharyngeo-vagal and the vago-hypoglosso-spinal, turn rostrally and run ventral to the mucosa between the mandible and the trachea. Along the intermandibular course, there is a short space in which the two roots are fused, but subsequent distribution does not indicate that there is any crossing of fibers.

5a. *Hyoglossus.* — (Synonymy: Zungenbeinmuskel, D'Alton, 1834). The hyoglossus is another long, thin band of muscle which is flat from its origin to the region of the tongue sheath, where it becomes more circular in cross-section. The fibers originate from the posterior tip of the hyoid apparatus and follow the rostro-medial course of the hyoid. Anteriorly, the muscle enters the tongue sheath and becomes the intrinsic muscle of the tongue (Albright & Nelson, 1959).

An element of the neurocostomandibularis, which arises posterior to the hyoid, partially inserts on the fascia of the hyoglossus in the ventral portion of the origin of the latter muscle. Fibers of the dorsal portion of the origin of the hyoglossus are continuous with the neurocostomandibularis. Only an inscription intervenes.

Location.—Ventral to the hyoid, oesophagus and trachea; between these structures and the neurocostomandibularis.

Origin.—From the posterior one-eighth of the hyoid apparatus. The origin surrounds the hyoid except for its midventral area. From the midventral area, half of the fibers are directed laterad and half mediad before they turn rostromediad and join ventral to the hyoid.

Insertion.—In the tongue sheath.

Innervation. — The glossopharyngeo - vagal nerve root, shortly after turning rostrad in the intermandibular region, gives off a fairly prominent branch of glossopharyngeal fibers, the lingual ramus. The lingual ramus follows the main root rostrad for some distance before turning mediad to send several small rami into the hypoglossus. The principal part of the lingual ramus proceeds rostrad along the dorso-lateral surface of the hyoglossus and into the tongue sheath, where it eventually embeds in the muscle. The intrinsic tongue muscles are also innervated by the lingual ramus of the inferior dentary nerve of the trigeminal (carrying chorda tympani fibers), which emerges from the beginning of the Meckelian sulcus in the splenial and joins an anterior ramus of the vago-hypoglosso-spinal nerve. Presumably the fibers from the vago-hypoglosso-spinal going to the tongue muscles are hypoglossal. A second, very small twig from the vago-hypoglosso-spinal nerve follows the anterior ramus into the tongue but does not fuse with the others.

Function.—Intrinsic tongue movements.

5b. *Hyotrachealis.*—(Synonymy: Rückwärtzieher des Kehlkopfs, D'Alton, 1834; hyoideolaryngeus, Bronn, 1890). (Text-fig. 1). The hyotrachealis is a long strap of muscle passing from the hyoid rostro-mediad to the larynx, dorsal to the geniotrachealis.

Location.—On the ventral surface of the mucosa of the mouth and oesophagus except in the region of its insertion, where it swings ventrad to the larynx. The muscle is dorsal to the neurocostomandibularis and crosses the geniotrachealis dorsally. At the origin of the muscle, the pterygoideus lies between it and the mucosa.

Origin.—From the rostro-lateral face of the hyoid apparatus.

Insertion.—On the ventro-lateral and ventral faces of the laryngeal cartilages. The pair of hyotracheales almost meet midventrally.

Innervation.—Posterior to the point of fusion of the vago-hypoglosso-spinal and the glosso-pharyngeo-vagal nerves in the intermandibular region, the vago-hypoglosso-spinal nerve gives off a small ramus. The ramus sends very fine but long twigs to connective tissues around the blood vessels of the region and then continues medially to innervate the hyotrachealis. Anterior to the area of fusion, the glossopharyngeo-vagal nerve sends very small branches into the hyotrachealis. It may be that the ramus from the vago-hypoglosso-spinal nerve, since it does have fibers going to connective tissue and/or blood vessels, is autonomic (Xth) and not motor.

Function.—Either retraction of the larynx or protraction of the hyoid, depending on the action of associated muscles.

Variations.—The origin of the hyotrachealis from the hyoid may be confined to a few fibers with the majority of the fibers arising from an inscription in the neurocostomandibularis. The inscription is rostro-lateral to the origin of the fibers from the hyoid. Some fibers do not originate in this area but come from some point far caudal (the head was severed too far anteriorly to be able to follow these fibers to their origin. CNHM 31700). Although individual fasciculi could be followed for some distance caudad, the hyotrachealis was not entirely separable from the neurocostomandibularis posterior to the hyoid.

There may be a coalescence of fibers of the geniotrachealis and hyotrachealis.

5c. *Genioglossus.* – (Synonymy: Vorwärtzieher des Zungenbeins, D'Alton, 1834; maxillo-hyoideus, Bronn, 1890). The genioglossus is a long muscle stretching caudo-medially from the anterior tip of the dentary to the posterior extremity of the tongue sheath. It is flattened between the tongue sheath and the geniotrachealis. The original area on the dentary is small, but at the insertion the muscle fans out, almost surrounding the tongue sheath. Since some of the fibers insert on the fascia of the hyoglossus, they give the appearance of being continuous with the hyoglossus, but no fusion occurs.

Location.—This is a muscle of the deep, anterior intermandibular region. The anterior quarter of the genioglossus lies between the two heads of the anterior intermandibularis for the most part, with only a small portion of the dorsal surface in contact with the geniotrachealis. Caudally, the geniotrachealis swings slightly ventrad to lie lateral to the compressed genioglossus, leaving the dorsal surfaces of both muscles in contact with the mucosa. The middle third of the genioglossus is covered with the mucosa. The middle third of the genioglossus is covered ventrally by the insertion of the intermandibularis posterior ventralis. Here the genioglossus adheres closely to the tongue sheath, as it does for the remainder of its length.

Origin.—On the ventro-medial plane of the anterior curved tip of the mandible.

Insertion.—On the tongue sheath, from the level of the posterior mylohyoid foramen (Oelrich, 1956) in the angular caudad to the level of the last labial. In this area the fascia of the genioglossus merges with the tongue sheath. The insertion covers the tongue sheath from the mid-ventral to almost the mid-dorsal line.

Innervation.—The anterior termination of the vago-hypoglosso-spinal nerve root is a number of anterior rami of hypoglossal fibers located postero-lateral to the larynx. One of these anterior rami turns sharply mediad, anterior to the combined lingual ramus of the trigeminal and an anterior ramus of the vago-hypoglosso-spinal, and sends branches into both the genioglossus and geniotrachealis.

Function.—Protracts the tongue sheath.

Variations.—A small slip of the genioglossus may separate from the main muscle mass and insert on the tongue sheath anterior to the rest. This slip is enclosed by the fascia of the tongue sheath for some distance before its insertion.

5d. *Geniotrachealis.*—(Synonymy: Vorwärtszieher des Kehlkopfs, D'Alton, 1834; maxillo-laryngeus, Bronn, 1890). The geniotrachealis is a much elongated muscle, circular in cross-section, which has fibers directed caudo-mediad, closely paralleling the genioglossus. At its origin it is almost completely encased by the two heads of the intermandibularis anterior. Only small ventral and dorsal areas are adjacent to the genioglossus and the mucosa of the mouth, respectively.

Location.—This is another muscle of the deep, anterior intermandibular region. The middle portion of the geniotrachealis is ventral to the mucosa and the mandibular gland, while the posterior portion passes ventral to the hyotrachealis also. It is dorsal to the neurocostomandibularis, intermandibularis anterior and genioglossus, as well as portions of the intermandibularis posterior dorsalis and ventralis.

Origin.—From the dentary on the medial surface just ventral to the second or third tooth socket.

Insertion.—On the lateral and dorso-lateral

and dorsal walls of the trachea between the levels of the anterior mylohyoid foramen in the splenial and the posterior mylohyoid foramen in the angular.

Innervation.—Three of the anterior rami of hypoglossal fibers from the vago-hypoglosso-spinal nerve turn mediad to innervate the geniotrachealis. The most anterior ramus also sends branches to the genioglossus.

Function.—Protracts the larynx

Variations.—The geniotrachealis varies from a simple column of muscle to a complex of branching segments and coalescing fibers. The fibers of the geniotrachealis and hyotrachealis may unite where the two muscles are in contact. Anterior and dorsal to this, the geniotrachealis may be joined by a dorsal segment which is as large as the principal part of the muscle. The dorsal segment arises from the dentary just dorsal to the origin of the main element of the muscle. Many fibers insert on the mucosa postero-medial to the mandibular gland, intermingling with fibers from a fasciculus of the intermandibularis posterior dorsalis, to which they seem to fuse but do not. Most of the fibers of the dorsal segment join the main head near its insertion. Near the anterior end of the mandibular gland, two prominent fasciculi leave the dorsal segment and are directed caudo-laterad to the mandibular gland. Fasciculus one and two originate from the dentary antero-dorsal to the origin of the main portion of the geniotrachealis and its dorsal segment and from the mucosa immediately caudo-dorsal to this area. The fibers of fasciculus one and the dorsal segment unite in this region. The fibers of fasciculus one pass caudad over the ventral surface of the mandibular gland and some become embedded in the fibrous capsule of the gland while others, after passing dorsad around the postero-medial end of the gland, turn anteriorly and fan out to insert on the mucosa dorsal to the gland. One group of fibers from fasciculus one maintains a more medial course, not passing closely around the end of the gland, but curving broadly to insert on the mucosa dorsal and dorso-medial to the gland. This insertion meets that of a portion of the intermandibularis posterior dorsalis and the two muscles form a cup in which the posterior portion of the gland lies.

Fasciculus two lies dorsal to fasciculus one and their fibers follow a parallel course until the posterior third of the mandibular gland is reached. There, fasciculus two curves sharply laterad, closely applied to the gland, and encircles the gland almost completely, to insert on the dorso-medial face of the gland sheath. The gland, its sheath and the glandular head of the intermandibularis posterior dorsalis are enclosed by fasciculus two. A small portion of the fibers from fasciculus two follows fasciculus one and inserts in the mucosa dorsal to the gland.

5e. *Neurocostomandibularis.* – (Synonymy: Nackenunterkiefermuskel (part) and Kieferzungenbeinmuskel (part), D'Alton, 1834; neuro-mandibularis, costo-mandibularis, and mylohyoideus, Owen, 1866; Phisalix, 1922; cervico-mandibularis and mylohyoideus, Bronn, 1890; neuro-mandibularis and costomandibularis, Radovanovic, 1935; neuro-mandibularis, rectus system, and branchiomandibularis spinalis, Lubosch, 1938; vertebro-mandibularis, costo-mandibularis, and mylohyoideus, Anthony & Serra, 1950). (Text-figs. 1 & 2). This is a complex muscle with numerous origins and insertions. It covers the lateral cervical, throat, and intermandibular regions and is superficial except for the constrictor colli, the superficial head of the intermandibularis posterior ventralis, and a portion of the retractor quadrati.

The aponeurosis by which the neurocostomandibularis inserts on the mandible lies medial to the aponeurosis of the cervicomandibularis. Most of the neurocostomandibularis aponeurosis inserts on the lateral face of the dentary and compound bone ventral to the infralabial gland, and along this portion of its insertion it is fused with the cervicomandibularis aponeurosis. At the two extremities of the gland, the neurocosto-mandibularis aponeurosis passes medial to the gland and at the angle of the mouth it fuses with the submucosa. Anterior to the gland the two aponeuroses fuse and attach to the dentary.

Of the various heads, vertebral, hyoid, costal and cutaneous, described for *Thamnophis* (Cowan & Hick, 1951) and *Elaphe obsoleta* (Albright & Nelson, 1959), only the vertebral and costal heads are discrete in *Boa constrictor*. In the throat region there is no distinct separation of body musculature and the neurocosto-mandibularis.

There are two well-defined inscriptions, the anterior one located at about mid-point on the hyoid apparatus, and a complex, more posterior one found at the posterior tip of the hyoid. The complex is pectinate and lies at an angle running antero-dorsad from the hyoid to the region of the retroarticular process, bisecting the vertebral head. There are three small offshoots of the main inscription which receive numerous fasciculi from several different muscles and tend to divide the vertebral head into layers. The dorsal offshoot receives four different muscle bundles: a slip from the medial surface of the retractor

quadrati, costal head of the neurocostomandibularis, vertebral head, and a bundle which passes anteriorly to the intermandibular section of the neurocostomandibularis. The two ventral offshoots receive all of these plus fasciculi from the costocutaneous superior. The inscription continues antero-mediad from the posterior tip of the hyoid almost to the midventral line. This part of the inscription does not branch. Near the posterior tip of the hyoid, fasciculi from the retractor quadrati, costal head of the neurocostomandibularis (but not from the vertebral head), costocutaneous superior, and a segment which goes anteriorly to the intermandibular section of the neurocostomandibularis attach to the unbranched portion of the inscription complex. Some of the fibers of the intermandibular part of the neurocostomandibularis, which arise from the inscription complex, insert on the hyoid and the rest on the anterior inscription. A few may continue across the anterior inscription to the aponeurosis, but the inscription appears to bisect the fibers of the intermandibular region completely and anchor medially to the anterior edge of the first rib.

The innervation of the neurocostomandibularis indicates that this is a composite muscle, as is suggested by the extensiveness of the muscle and the inscriptions within it. The fibers of the neurocostomandibularis in the mandibular region (that is, anterior to the posterior inscription, and between the hyoid and mandible) are supplied by branches from the glossopharyngeo-vagal nerve. Near the point where the nerves and vessels turn rostrad into the intermandibular area, the fibers are innervated by a long, fairly large nerve which arises near the petrosal ganglion. Because of the fusion of the nerve roots, it was not clear whether the long ramus came from the glossopharyngeo-vagus or the vago-hypoglosso-spinal nerve. It is likely that the ramus is composed either of vagus or spinal nerve fibers. The vertebral head, costal head, and the fibers of the neurocostomandibularis lying postero-medial to the hyoid are innervated by spinal nerves.

Vertebral Head.—This head is found in the lateral cervical region posterior to the cervicomandibularis. The fibers, coming from a dorsal aponeurosis, converge slightly as they pass antero-ventrad around the retroarticular process into the intermandibular area where they become indistinguishable from fibers from other origins.

Origin of Vertebral Head.—On an aponeurosis from the neural crests of the eighth to the thirteenth vertebrae. The aponeurosis covers the spinal-semispinalis muscles.

Insertion of the Vertebral Head.—On the inscription complex, or, if the inscription is interpreted as interrupting but not terminating the fibers, the insertion would then be by the aponeurosis attached to the mandible.

Innervation of the Vertebral Head.—Branches of the fifth and sixth spinal nerves enter the ventral surface near the posterior inscription.

Costal Head.—The costal head is a deep-lying portion of the muscle, occupying a position from the twelfth rib anterior to the inscription complex and medial to the vertebral head and the costocutaneous superior. The medial surface of the costal head is adjacent to the oesophagus. The costal head represents the anterior fiber bundles of the costocutaneous inferior which, in the body region, arise from the tips of the ribs and proceed craniad to insert on the fascia of the medial surface of the costocutaneous superior. From the twelfth rib forward the insertion is changed, forming the costal head even though no definite fascial space separated this head from the costocutaneous inferior proper. The fibers arising from each rib remain discrete bundles, making it possible to determine the extent of the two muscles.

Origin of the Costal Head.—From the extreme tips of the first twelve ribs.

Insertion of the Costal Head.—From the first eleven ribs, the fiber bundles pass craniad to insert on the inscription complex. The fibers from the twelfth rib insert on the medial surface of the posterior tip of the hyoid. This insertion separates this bundle from both the costocutaneous inferior and the costal head but has been included with the costal head here for the sake of convenience.

Innervation of the Costal Head.—The rami of the spinal nerves, beginning with the fifth, passing over the medial surface of the costal head, give off very fine twigs to the muscle. The fifth to the tenth spinal nerves follow this pattern, but the number of nerves involved undoubtedly varies.

Intermandibular Portion of the Neurocostomandibularis.—The term, intermandibular portion, while admittedly unsatisfactory, is used in the absence of definable heads and delimitations from the body musculature. As used here, it will include the area between the mandibles and back to the posterior end of the hyoid.

The costocutaneous superior is a large mass of body muscle formed by bundles running from the lateral surface of the ribs caudad to the lateral edges of the gastrosteges. Anterior to the ribs, the origins are switched to various structures. Two bundles arise from offshoots of the

inscription complex, and larger groups of fibers come from the ventro-medial part of the main line of the inscription complex, the hyoid, and the anterior inscription.

There is so much fusion of fibers from this muscle and the intermandibular portion of the neurocostomandibularis that no distinction can be made and origins and insertions become confused. Fibers of the lateral part of the intermandibular portion begin at the inscription complex and proceed craniad to the aponeurosis, but toward the midventral line they arise from the hyoid and fuse rostrally with other fibers which lie between gastrosteges, posteriorly, and the anterior inscription or hyoid, anteriorly.

Innervation of the Intermandibular Portion of the Neurocostomandibularis.—The nerve supply for the neurocostomandibularis medial and anterior to the posterior inscription is varied. Postero-medial to the hyoid, it is innervated by the fifth, sixth and seventh spinal nerves. Since the transition from neurocostomandibularis to costocutaneous superior is gradual, it is impossible to say how many more spinal nerves are involved. The area dorso-lateral to the point where the nerves and vessels turn rostrad into the intermandibular region is supplied by the long ramus which arises from the nerve roots just posterior to the petrosal ganglion.

Function of the Neurocostomandibularis.— Primarily a depressor of the mandible. However, when the mandibles are held stationary with the teeth embedded in the prey, the action of the muscle is more complicated. As the head of the prey is moved from the buccal cavity into the oesophagus, the mandibular action is supplanted by contraction of throat muscles. Whereas the skin and intermandibular muscles have been relaxed to permit the extensive stretching necessary to get the prey in the mouth, now the intermandibular portion of the neurocostomandibularis contracts, bringing the skin and hyoid apparatus forward over the prey. Because of the lateral flare of the posterior part of the hyoid, the action produces a constriction of the throat laterally, leaving the ventral part free to stretch over the prey and not constricting the total diameter, which would tend to expel the prey. The laterad and dorsad swing of the posterior tip of the hyoid is augmented by the contraction of the retractor quadrati. The costal head of the neurocostomandibularis pulls the tips of the anterior ribs forward and outward, enlarging the diameter of the oesophagus either so that food can slip on down, or, after the head of the prey has passed this point, to get a "grip" on the prey in order to pull it further into the oesophagus. After the head of the prey has passed the first ribs, the costocutaneous superior, anterior part, is also used in pulling the skin forward over the prey.

Variations of the Neurocostomandibularis.— The costal head may involve varying numbers of ribs and the bundles from the ribs may not be discrete, in which case the fasciculi inserting on the offshoots of the inscription complex are not so well defined and the whole costal head tends to be inserted on the inscription medial to the vertebral head. This almost eliminates the overlapping layers of the vertebral head. The number of offshoots which receive fasciculi from the costocutaneous superior may vary. It may be that age determines how well defined the branches of the inscription complex are; in the older snakes the additional growth of connective tissue may obscure the original pattern.

The exact number of branches of the inscription complex receiving fasciculi from the retractor quadrati was most difficult to determine and may be variable.

5f. *Retractor quadrati.* — (Synonymy: Rückwärtzieher des quadratum, D'Alton, 1834; cervico-squamosal, Phisalix, 1922; cervico-supratemporal, Anthony & Serra, 1950). (Text-figs. 1 & 2). This muscle of the lateral cervical region forms a strong fibrous cord proximally, which lies deep to the cervicomandibularis, and a superficial fan-shaped distal area. The distal portion overlies the neurocostomandibularis and the inscription complex. The fibers radiate postero-ventrad, ventrad and rosto-ventrad.

Medially, the retractor quadrati gives off an element which subdivides into four or five very thin fasciculi. The fasciculi enter the vertebral head of the neurocostomandibularis at different levels and insert on the inscription complex. (See neurocostomandibularis).

Location.—Proximally, the retractor quadrati is embedded in the depressor mandibulae; the middle section is deep to the cervicomandibularis and its anterior edge is in contact with the nerves and blood vessels emerging from the cervical region. Distally, the muscle is superficial to the neurocostomandibularis except where the medial fasciculi penetrate it.

Origin.—By a short tendon from the proximal end of the postero-lateral face of the quadrate near its medial border.

Insertion.—On fascia attached to the skin which follows the contours of the hyoid and on the skin.

Innervation.—The third and fourth spinal nerves send rami laterad in the triangular area of fascia, vessels and nerves located posterior to the retroarticular process. The rami from the two spinal nerves branch medial to the retractor

quadrati and the branches coalesce before entering the muscle. The fifth spinal nerve pierces the retractor quadrati but does not supply the muscle.

Function.—The retractor quadrati supplements the action of the intermandibular portion of the neurocostomandibularis and constrictor colli in pulling the skin of the lateral neck region and hyoid upward and forward over the prey. It is doubtful that this muscle actually retracts the quadrate because of the position of the origin.

Variations.—The number of fasciculi entering the vertebral head of the neurocostomandibularis varies, or it may be that in smaller specimens the fasciculi are so small that they are missed.

Summary

The adductor mandibulae externi do not exhibit the degree of differentiation that is found in Colubrid snakes (Albright & Nelson, 1959; Cowan & Hick, 1951). There is some fusion of fibers in the dorsal area of the adjoining surfaces of the adductor mandibulae externus medialis and profundus. The adductor profundus is separated from the underlying adductor posterior only in the region in which the nerve V_3 penetrates. There is no protractor quadrati formed in *Boa constrictor*. The intermandibular posterior dorsalis and the geniotrachealis develop segments which insert on the mucosa dorsal, dorsolateral and dorso-medial to the mandibular gland. The segments form a depression in which the posterior portion of the gland fits. The geniotrachealis also has segments which surround the posterior half of the gland and attach to it. The intermandibularis posterior dorsalis also forms a glandular head which inserts directly to the caudal end of the gland. A very thin, obscure, superficial head of the intermandibularis posterior ventralis follows the course of the rest of the muscle but lies ventral to the neurocostomandibularis. A constrictor colli was found in all specimens examined. In the region of the posterior attachment of the zygomatic ligament, the cervicomandibularis forms several separate heads. They insert on the aponeurosis and on the quadrato-mandibular articulation capsule. The costocutaneous superior takes its origins from the ribs and courses caudad to insert on the gastrosteges. Anterior to the ribs, the origins are shifted to the inscriptions in the neurocostomandibularis and the hyoid. The more medial portions of the muscle fuse with the intermandibular portion of the neurocostomandibularis making separation of the two muscles impossible. The retractor quadrati forms several small medial slips which penetrate the neurocostomandibularis and insert on the inscription complex in that muscle. The inscription complex also receives heads from the costocutaneous inferior and the costocutaneous superior.

The innervation of the adductores mandibulae is afforded by seven rami which separate from V_3 just before or just after it emerges from the posterior trigeminal foramen. One ramus is the adductor superficialis nerve; three constitute the adductor medialis nerve; one is the pseudotemporalis nerve; one is the adductor profundus and posterior nerve, and one is the pterygoideus nerve. The three rami constituting V_4 separate from V_3 within the cranium and emerge from small foramina ventral and rostro-ventral to the posterior trigeminal foramen. These rami are the retractor pterygoidei and retractor vomeris nerve, the protractor pterygoidei nerve and the protractor and levator pterygoidei nerve.

The main ramus of V_3 enters the mandibular canal to become the inferior dentary nerve. A branch of the inferior dentary nerve, the intermandibularis-cutaneous nerve, leaves the canal by way of the foramen in the splenial to supply the intermandibularis anterior and posterior, dorsalis and ventralis, and the skin.

The hyoid musculature—that is, the depressor mandibulae, cervicomandibularis and constrictor colli—is innervated by rami which diverge, along with the chorda tympani, from the facial nerve in the region just medial to the columella.

Innervation of the hypobranchial-spinal musculature because of mixing of the fibers of the glossopharyngeal, vagus, accessorious, hypoglossal and spinal nerves is confusing. There is much doubt as to the origin of the fibers making up the rami to the muscles. A lingual ramus from the glossopharyngeo-vagal nerve trunk supplies the posterior region of the hyoglossus while a ramus formed from the fusion of a ramus lingualis lateralis (from the vago-hypoglosso-spinal trunk) and a lingual ramus (from the inferior dentary nerve) enters the intrinsic muscles of the tongue more anteriorly. Twigs from both the vago-hypoglosso-spinal and the glossopharyngeo-vagal trunk enter the hyotrachealis. Hypoglossal fibers from the vago-hypoglosso-spinal trunk supply both the genioglossus and the geniotrachealis. The neurocostomandibularis receives nerves from several sources: spinal nerves, a ramus from the glossopharyngeo-vagal trunk and a long ramus, which originates just posterior to the petrosal ganglion. Because of fusion of nerves in the region of the petrosal ganglion, it could not be determined whether the long ramus arose from the glossopharyngeo-vagal or the vago-hypoglosso-spinal trunk. The retractor quadrati is innervated by spinal nerves.

The constrictores dorsales control movements of the visceral skeleton. The adductores mandibulae assist in the rotation of the mandible on its longitudinal axis, as well as adducting the mandible. The constrictores ventrales constrict and elevate the floor of the mouth and adduct the mandibles towards the midventral line. The hyoid musculature depresses the lower jaw and contracts the throat region. The hypobranchial-spinal musculature provides movement for the larynx, intrinsic and extrinsic movements of the tongue, abduction of the mandible and hyoid and contraction of the skin.

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